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Dr. Diane Wickland
NASA Headquarters
300 E. St. SW
Washington, D.C. 20546
Code YSE

Dear Dr. Wickland,

Enclosed is my final report for my grant entitled "Predicting Photosynthetic Fluxes from Spectral Reflectance of Leaves and Canopies" (#NAGW-3707). This has been a very productive and successful project, and I am grateful for the funding NASA has provided. The main hypothesis, that photosynthetic function can be derived from "physiological reflectance indices" derived from spectral reflectance of leaves and canopies, continues to be supported, and is leading to an interesting variety of new applications and science results. Eight papers (four journal papers submitted or published, and four conference papers) have resulted to date, with several more manuscripts now approaching completion.

The technical and biological innovations developed with NASA support have also led to some promising ties with industry. PP Systems of Haverhill MA is now marketing a new, low-cost spectrometer (the "UniSpec") with foreoptics and software specifically designed for ecological and physiological studies. The UniSpec is a modified design of one of my prototype spectrometers (the "leaf reflectometer") developed during this grant. This instrument enables reliable laboratory or field reflectance measurements of narrow-leaved plants (e.g. conifers and chaparral species), and will undoubtedly open up new opportunities for linking spectral reflectance to physiological function.

In addition to positive science results and technical advances, many Cal State students have benefited through improved training and research opportunities, and several spinoff projects (many student projects involving spectral reflectance) are emerging. Additionally, the resources and capabilities developed during the life of this grant are now enabling me to more fully apply imaging spectrometry to large-scale ecological studies, and are allowing me to participate in teaching and public outreach efforts involving AVIRIS and other NASA image products.

I understand that you might be coming to the Pasadena area towards the end of February for a JPL site visit. Should you have time in your schedule, I would like to extend an invitation for you to visit our campus, which is a short distance from JPL. I would welcome the opportunity to introduce you to some of the current activities on campus relating to remote sensing research, student training, and public outreach.

Thanks again for the support.

Sincerely, 

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Summary of results

Science results

The central hypothesis of this study has been that photosynthetic efficiency and capacity can be predicted from "physiological reflectance indices" derived from spectral reflectance of leaves and canopies. I have approached this topic with a combination of laboratory and field experiments, and have also explored the potential of deriving a meaningful physiological index from imaging spectrometry (e.g. AVIRIS). A few highlights are presented below.

The main emphasis has been on the "Photochemical Reflectance Index" (PRI), derived from reflectance at 531 nm and 570 nm. Unlike most "conventional" vegetation indices (e.g. NDVI), PRI changes rapidly both with illumination and physiological state (figures 1 & 2), because it detects the interconversion of xanthophyll cycle pigments, which serve as photoregulatory pigments and control energy distribution for the photosynthetic system. This approach has differed dramatically from most remote sensing in that it has emphasized *temporal* variation in *narrow-band* spectral signatures, instead of spatial patterns of broadband indices. Our primary conclusion has been that PRI works well as an index of photosynthetic light-use efficiency at the leaf scale, much in the same way as the fluorescence index $\Delta F/F_m'$ (figures 3 & 4). However, unlike $\Delta F/F_m'$ which must be measured at close scales, PRI can be sampled at a range of spatial scales, presenting the possibility of monitoring photosynthetic fluxes remotely.

To explore the potential for remote sensing of photosynthetic function with this reflectance index, we sampled top canopy leaves of many species at midday. In this field study, PRI varied with light use efficiency ($\Delta F/F_m'$) and midday photosynthetic rates determined from actual carbon fluxes, even across many species (figure 4). In this study, species with chronically suppressed photosynthetic rates (e.g. drought-tolerant evergreens or nutrient-stressed plants) typically exhibited greater photosynthetic "downregulation" detectable as reduced PRI. These significant correlations between PRI and various measures of photosynthetic function for top-canopy leaves further supports the use of remote spectrometry for deriving photosynthetic fluxes.

The use of PRI as an index of photosynthetic downregulation and relative photosynthetic rates is further supported by additional field studies on ponderosa pine conducted in the summer of 1996 in collaboration with Dr. Barbara Yoder (Oregon State University). Dr. Yoder has been exploring differences in photosynthetic function in young and old trees associated with differences in hydraulic conductance, and has reported that old trees appear to "shut down" photosynthesis towards midday to a much greater degree than young trees (Yoder et al. 1994). When we examined PRI on these same trees, we found a dramatically lower PRI values for the old tree towards midday, reflecting the greater degree of downregulation in old trees (figure 5). These findings suggest that imaging spectrometry could be used to detect spatial variation in photosynthetic rates associated with different vegetation patches at the landscape scale.

To test the possibility of applying PRI as a remote index of photosynthetic function at scales larger than the leaf, we have begun a series of "scaling" experiments that examine reflectance simultaneously at leaf, canopy, and stand scales using ground-based spectrometers. In general, diurnal patterns of PRI at the canopy and stand scales, closely resemble those at the leaf scale, particularly for closed canopies and stands, suggesting that this index is detectable at a range of spatial scales. However, our experimental results to date (gathered in summer, 1996) indicate that canopy and stand structure (e.g. varying amounts of bare ground in the field of view) can complicate interpretation of this index at larger scales. Additionally, in collaboration with Joseph Berry (Carnegie Institution) and colleagues, we have sampled spectral reflectance at multiple spatial scales in conjunction with gas exchange and eddy correlation at a boreal forest jack pine site. The results from these scaling studies are still being analyzed, and should help us determine whether is

possible to reliably derive estimates of carbon flux from this index at scales larger than the single leaf. It is likely that further scaling experiments in conjunction with eddy correlation and modeling will be needed to fully resolve this question.

Determination of spatial and temporal patterns of light-use efficiency with spectral reflectance allows prediction of photosynthesis according to the following equation:

$$\text{photosynthetic rate} = \text{efficiency} \times \text{APAR} \quad (1)$$

We have found that both efficiency and APAR can be determined from spectral reflectance, combined with light measurements, presenting the exciting possibility of deriving photosynthetic fluxes from optical sampling alone. Initial model results and field sampling indicate the potential for this index to depict spatial patterns of photosynthesis within a canopy and across individuals in a stand (figures 5 and 6). Diurnal PRI patterns qualitatively similar to photosynthetic patterns can also be detected at the larger stand scale, but a clear physiological interpretation of this index remains elusive at this scale, in part due to the potentially confounding effects of canopy and stand structure on spectral reflectance (described above). Further field studies and canopy experiments are needed to resolve the influence of canopy and stand structure on this index.

One goal of this research was to examine the potential of extracting information about physiological function from AVIRIS imagery. It has been difficult to draw clear conclusions from these efforts, in part because most AVIRIS imagery is not optimally suited for experimental studies of PRI. In general, it has not been possible to control the time of AVIRIS overflights or to obtain multiple overflights in coordination with ground truthing measurements, and these are serious drawbacks for studies of temporally dynamic photosynthetic processes. This, combined with the relatively large pixel size of AVIRIS (relative to leaf and canopy scales, where PRI has been best studied), makes it difficult to develop direct, mechanistic relationships between AVIRIS imagery and ground studies. Despite these challenges, some promising results have emerged. While the earliest AVIRIS imagery was clearly too "noisy" to use for accurate PRI sampling, more recent imagery has attained a level of signal-to-noise suitable for exploring narrow-band imagery in PRI bands (531-570 nm). PRI derived from a 1992 AVIRIS overflight of the Jasper Ridge Biological Preserve yielded a spatially coherent image, with the PRI values of different vegetation patches matching the expected photosynthetic rates for those vegetation types (photosynthesis was based on separate studies, e.g. Gamon et al. 1995a). However, PRI was also clearly correlated with canopy or stand features measured by NDVI and green vegetation fraction (derived from spectral mixture analysis), making it difficult to assign a clear physiological significance to PRI at this scale. The results of these preliminary efforts have been presented in a pair of conference papers (Gamon et al. 1995 b&c). Although I continue to explore the potential for deriving photosynthetic rates from imaging spectrometry, my main efforts in the near future will continue to be to apply physiological indices at the leaf and canopy scales, where experimental tests can be most readily conducted.

Technical advances

Several key technical advances have been essential to the progress of this study. The development of a laboratory system for simultaneous measurement of gas exchange, spectral reflectance and fluorescence is a unique capability of our laboratory that has allowed us to explore the functional relationships between dynamic reflectance features and photosynthetic processes (see figure 2). Additionally, we have improved our leaf "reflectometer" so that it is now more portable and capable of resolving reflectance of leaves less than 0.5 mm in diameter in 1-3 seconds, allowing rapid and consistent reflectance measurement on virtually all terrestrial plant species. With this instrument, it is now possible to obtain accurate and repeatable reflectance measurements on narrow leaves

(e.g. conifer needles and leaves of chaparral species, as shown in figure 1) that have previously been "inaccessible" to reflectance sampling. These technical improvements have greatly facilitate our studies that seek a "universal" reflectance index of photosynthetic function (e.g. figure 4).

Related improvements in resources and infrastructure

During the period of NASA support, I have developed laboratory and horticultural facilities needed to complete this study. During this project we have constructed a fenced area by the Biological Sciences building for outdoor plant culture, and repaired a rooftop decking area now used for plant culture and canopy-level studies. Additional infrastructural improvements are planned, including greenhouse upgrades and facilities for controlled plant growth chambers, which should improve our ability to conduct controlled experiments. Parallel improvements are underway in the campus computer and image processing facilities. Recently, the "Center for Spatial Analysis and Remote Sensing" (CSARS) has been established on campus with NASA funding (Director: Dr. Ali Modarres). We are now assembling the hardware and software for "serious" remote sensing, image processing, and GIS studies. The addition of these computing facilities will benefit further work involving the application of imaging spectrometry to ecological studies.

Links to Industry

The research supported by this grant has led to productive links with industry. A commercial version of my prototype reflectometer (the "UniSpec" spectrometer) is now being manufactured by PP Systems of Haverhill, MA. I have acted as an unpaid "consultant" to PP Systems in the design and biological application of this instrument. In return, PP Systems has financed the development of new software and is currently providing me with an improved, portable prototype instruments for field and lab testing. To my knowledge, the UniSpec instrument is the first inexpensive (<\$10,000) field spectrometer complete with foreoptics and software specifically designed for ecological and physiological measurements.

Teaching and student training

Student training has been a central aspect of this research. During the period of this grant, 20 students, including 15 undergraduates, 5 masters students, and 2 visiting Ph.D. students have worked in my laboratory. Student training has primarily been in gas exchange, spectral reflectance, remote sensing and image processing, pigment analysis, scientific writing, and horticultural skills. One student has also received extensive training in climbing and safety for canopy research from towers. Students have been co-authors or authors on three peer-reviewed papers, three conference papers, and eight published meeting abstracts (primarily at the Ecological Society of America - see abstracts, below). Six additional publications (listed below) are in preparation, five with students as co-authors. Student authors and co-authors are indicated by asterisks (*) in the publications list below.

The skills and capabilities developed with funding from this grant has allowed me to introduce several students to the use of AVIRIS imagery for vegetation studies. AVIRIS data of the Santa Monica Mountains were used to teach image processing skills and remote approaches to vegetation sampling to 16 Cal State students who were enrolled in Biology 454 ("Instrumentation and Methods in Environmental Science") during the spring of 1996.

Collaborations

NASA support has also allowed me to continue effective collaboration with the following scientists outside of Cal State LA.

Dr. Barbara Yoder (Oregon State University)
 Dr. Christopher Field (Carnegie Institution)
 Dr. Dar Roberts (University of California, Santa Barbara)
 Dr. Joseph Berry (Carnegie Institution)
 Dr. Stephen Mulkey (University of Missouri)
 Dr. Susan Ustin (University of California, Davis)

These collaborations have taken me to Panama, Canada, and the Pacific Northwest and have enabled me to test the findings of laboratory experiments in a variety field settings. Additionally, during the period of this grant, I have hosted four visiting scientists (Dr. J. Peñuelas, Dr. I. Filella and L. Serrano from Barcelona, Spain; and Dr. K. Suh from Taegu University, Korea). Visiting scientists have been a tremendous asset to the lab, serving as additional mentors, role models, and friends for the many Cal State students who work with them.

Spinoff Projects

Several spinoff projects have emerged during the period of this study. Several students have applied spectral reflectance to studies of air pollution damage in white clover and yellow pine. A former undergraduate is now completing a Master's thesis on results of the clover study. Another student has used remote sensing techniques to study wildflower population dynamics. Several additional Cal State LA students completed summer projects at the US EPA lab in Corvallis, Oregon using spectral reflectance to assess pigment content under a range of nitrogen, CO₂ and ozone levels. Most of these projects have been presented as posters at the Ecological Society of America (see Published Abstracts, below), and additional manuscripts are currently in preparation from this work (see Manuscripts in Preparation, below).

Public Outreach activities made possible partly by this grant

As part of a separate effort (the "Urban Environment Initiative,"* led by Cal State faculty members Drs. Ali Modarres and Hong-Lie Qiu), I have been working to make NASA image products available to public groups. My role in this project has largely been to provide AVIRIS image products of the Santa Monica and Santa Susana Mountains to local public groups. For example, the Santa Monica Mountains Conservancy is interested in the possibility of using AVIRIS-derived vegetation maps of these areas for planning wildlife corridors. Another group ("Tree People" and the consulting firm Re-Think) has become interested in the possibility of using hyperspectral imagery for mapping urban vegetation. The skills and capabilities developed with funding from my NASA grant is now making possible the dissemination of AVIRIS data products to these public groups.

* The Urban Environment Initiative is a partnership involving NASA's Minority University Space Interdisciplinary Network (MU-SPIN), Prime Technologies Service Corporation, California State University, Los Angeles, and Central State University (Wilberforce, Ohio). The goal is to assist public groups in using the products of NASA technology for local, environmental problem solving.

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- Gamon JA, Serrano L, Surfus JS (in review) The photochemical reflectance index: an optical indicator of photosynthetic radiation-use efficiency. Oecologia
- Gamon JA, Yoder B (In preparation) Midday photosynthetic downregulation detected by narrow-band reflectance in mature Douglas-fir and ponderosa pine trees. *Note: results in this manuscript are also being presented at the 1997 ESA meeting , 11-14 August, Albuquerque, New Mexico.*
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR (1994) Evidence of reduced photosynthetic rates in old trees. Forest Science 40(3):513-527.

Publications

To date, four peer reviewed papers (published or submitted), four conference papers, and seven meeting abstracts have resulted from this research. An additional six manuscripts are in preparation, and I expect most of these to be submitted during 1997. Papers and abstracts with student authors or co-authors are indicated with an asterisk (*). Note: the lists below only include work directly related to and supported by this NASA funding, and do not include additional publications completed during the period of this grant.

Peer-reviewed papers published or submitted

*Gamon JA, Serrano L, Surfus JS (in review) The photochemical reflectance index: an optical indicator of photosynthetic radiation-use efficiency. Oecologia

*Serrano L, Gamon JA, Berry J (in review) Estimation of leaf area with an integrating sphere. Tree Physiology.

Peñuelas J, Filella I, Gamon JA (1995) Assessment of photosynthetic radiation-use efficiency with spectral reflectance, New Phytologist 131:291-296.

Gamon JA, Field CB, Goulden M, Griffin K, Hartley A, Joel G, Peñuelas J., Valentini, R (1995) Relationships between NDVI, canopy structure, and photosynthetic activity in three Californian vegetation types. Ecological Applications. 5(1):28-41.

Conference Papers Published

*Gamon JA, Serrano L, Roberts DA, Ustin SL (1996) A ground truthing method for AVIRIS overflights using canopy absorption spectra. In: Green RO (Ed) Proceedings of the Sixth Annual JPL Airborne Earth Science Workshop, Pasadena, 4-8 March 1996. JPL Publication

*Gamon JA, Green RO, Roberts DA, Serrano L (1995) Deriving photosynthetic function from calibrated imaging spectrometry. In: Guyot G (Ed) Proceedings of the International Colloquium, Photosynthesis and Remote Sensing, 28-30 August, Montpellier, France. pp. 55-60.

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Gamon JA, Roberts DA, Green RO (1995) Evaluation of the photochemical reflectance index in AVIRIS imagery. In: Green RO (Ed) Proceedings of the Fifth Annual JPL Airborne Earth Science Workshop, Pasadena, 23-26 January 1995. JPL Publication 95-1:55-58.

Manuscripts in preparation

- *Gamon JA, Berry J, Fredeen AL, Serrano L. Vertical gradients of photosynthetic radiation-use efficiency in boreal forest trees detected by optical measurements
- Gamon JA, Field CB, Fredeen AL, Thayer S, An optically-based photosynthesis model: initial results from a sunflower canopy
- *Gamon JA, Mulkey S, Serrano L, Wright J, Diverse canopy physiology and morphology assessed by optical measurements during the dry season in a neotropical forest.
- *Gamon JA, Olszyk D, Tefera K Needle reflectance and transmittance measurements as indicators leaf nitrogen content in Douglas-fir
- *Gamon JA, Surfus JS, Assessing xanthophyll pigment content and light history with spectral reflectance kinetics.
- Gamon JA, Yoder B, Midday photosynthetic downregulation detected by narrow-band reflectance in mature Douglas-fir and ponderosa pine trees.

Published abstracts (conference proceedings)

- *Surfus JS, Garcia D, Gamon JA (1996) Quantifying ozone damage to pine needles using a leaf reflectometer. Ecological Society of America, Providence, Rhode Island, 10-14 August, 1996.
- *Fuentes D, Garcia D, Surfus J, Gamon JA (1996) A white clover bioassay that tracks seasonally changing ozone levels. Ecological Society of America, Providence, Rhode Island, 10-14 August, 1996.
- *Gamon JA, Surfus JS, Choi I-L (1996) Monitoring photosynthetic activity with spectral reflectance: evidence for two reflectance signals. Ecological Society of America, Providence, Rhode Island, 10-14 August, 1996.
- *Tefera K, Gamon JA, Olzsyk D (1996) Effects of nitrogen, elevated CO₂ and temperature on Douglas-fir leaf reflectance. Ecological Society of America, Providence, Rhode Island, 10-14 August, 1996.
- Suh K, Gamon JA (1995) The relationship between photosynthetic light use efficiency and the photochemical reflectance index. Ecological Society of America, Snowbird, Utah, 30 July - 3 August, 1995.
- *Flower LS, Gamon JA. (1994) Estimation of wildflower population density and distribution with spectral mixture analysis. Ecological Society of America, Knoxville, Tennessee, August 1994.
- *Serrano L, Nazir MA, Surfus JA, Gamon JA (1994) Estimation of leaf area index and absorbed photosynthetically active radiation with spectral absorptance. Ecological Society of America, Knoxville, Tennessee, August 1994.

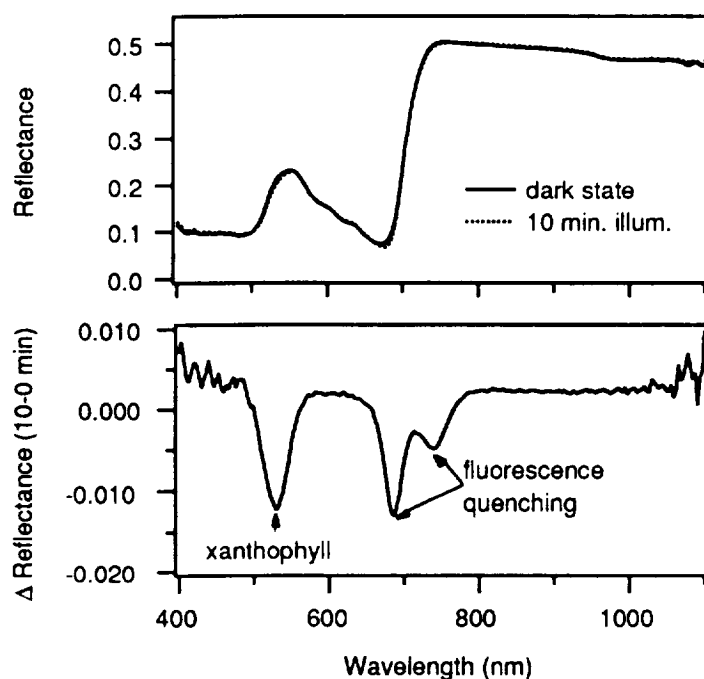


Figure 1. Panel A: Reflectance of a single Douglas-fir needle sampled in the dark state (solid line) and 10 minutes after continuous illumination with the equivalent of full sunlight (dashed line). Changing illumination causes subtle changes in apparent reflectance on the left side of the "green hump" at 550 nm and in the vicinity of the "red edge" at 700 nm. Panel B: The difference spectrum (reflectance in the light state minus reflectance in the dark state) reveals a clear feature at 531 nm associated with the conversion of the xanthophyll cycle pigments to zeaxanthin and a double feature near 700 nm due to chlorophyll fluorescence quenching. The photochemical reflectance index (PRI) is an expression of the dynamic 531 nm xanthophyll feature, normalized against the right edge of this feature at 570 nm. Normalizing R_{531} against R_{570} reduces complications of varying illumination, sampling geometry, leaf or canopy structure, and pigmentation (Gamon et al. 1992, 1993). Both chlorophyll fluorescence and PRI can be used to assess rapidly changing light-use efficiency and derive estimates of photosynthetic carbon uptake, as described below. This needle was sampled with our portable "reflectometer" (described under "Technical Advances," above) from the Wind River Canopy Crane, Carson WA, in September 1996.

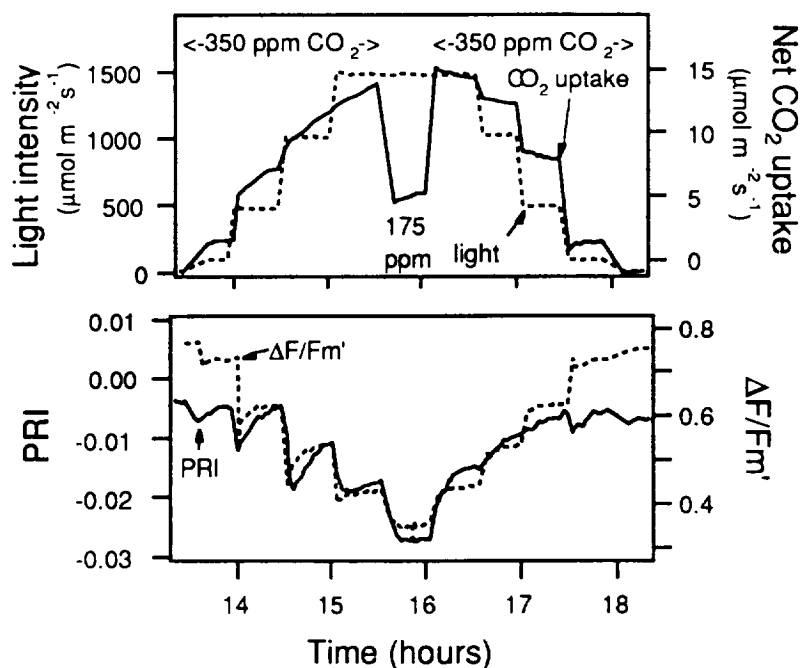


Figure 2. Lab experiment on a cotton leaf combining steady-state leaf gas exchange with reflectance and fluorescence sampling. Reflectance (PRI) and fluorescence ($\Delta F/F_m'$) are continuously sampled using fiber optic probes directed at the leaf positioned in a gas exchange chamber. Environmental conditions (e.g., light intensity and CO_2 concentration) can be varied independently (top panel). In this case we simulated a diurnal light exposure with a midday stomatal closure event, causing measurable effects on leaf optical signals (bottom panel). In all but the lowest light levels, good correlations exist between PRI, $\Delta F/F_m'$ and efficiency derived from gas exchange (figure 3), supporting the use of PRI as an index of light-use efficiency under typical illumination conditions of remote sensing. From Gamon et al. (in review).

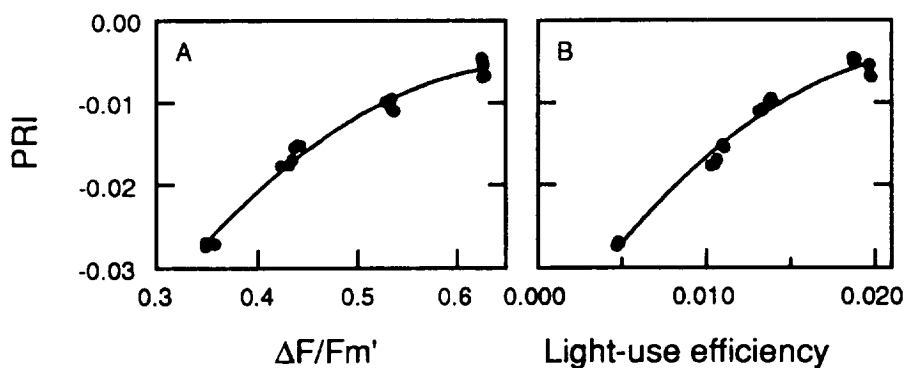


Figure 3. Relationship between PRI and two measures of photosynthetic light use efficiency derived from laboratory experiment with widely varying light intensity and CO_2 concentration (see figure 2). Points indicate samples at medium-to-high light (light intensity $> 100 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$). $\Delta F/F_m'$ (panel A) is a fluorescence index of PSII light-use efficiency, and "light-use efficiency" (panel B) represents the net CO_2 uptake rate divided by the incident light intensity. From Gamon et al. (in review).

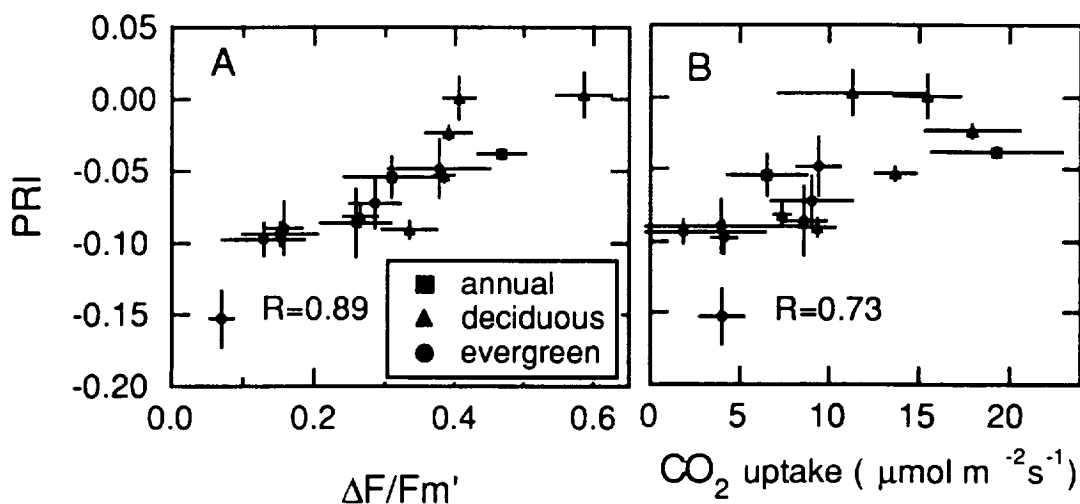


Figure 4. Relationship between PRI, $\Delta F/Fm'$, and midday photosynthetic rate (net CO_2 uptake) for fifteen species representing three functional types (see legend). Top canopy leaves were sampled in full sun at midday in Los Angeles, CA, to mimic the "view from above" typically sampled by remote spectrometers. $\Delta F/Fm'$, a fluorescence-based index of PSII light-use efficiency, was measured immediately after PRI, whereas photosynthetic rates were measured several days later under similar high light conditions. Because sunlight levels were nearly constant during midday sampling, the correlation between PRI and light-use efficiency is very similar to panel B (not shown). The significant correlation between PRI and CO_2 uptake for these upper-canopy leaves suggest that it should be possible to detect photosynthetic downregulation with remote spectrometry. From Gamon et al. (in review).

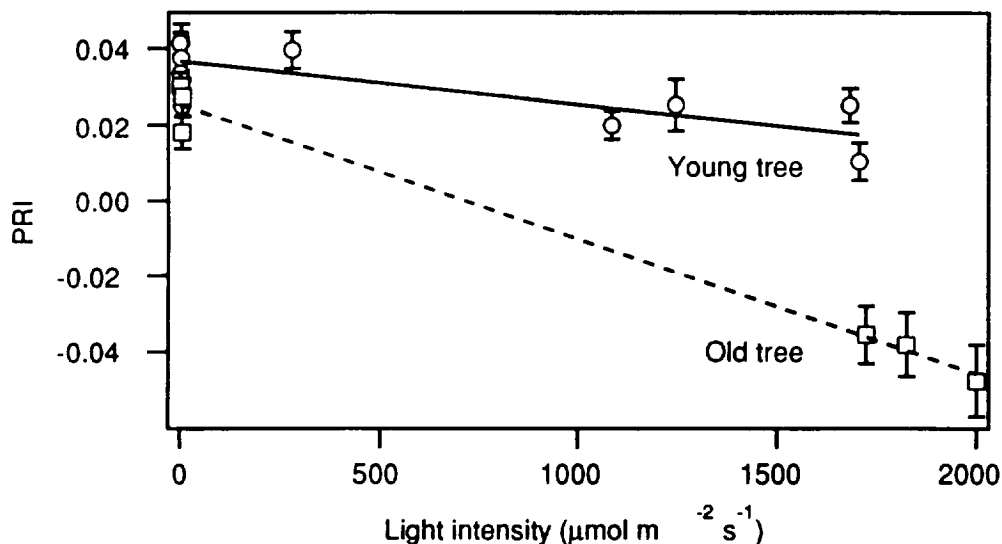


Figure 5. Contrasting PRI light responses for young and old ponderosa pine trees at Black Butte, OR, sampled in September, 1996. Each point represents the mean (\pm SEM) of 9 needles. The light response was determined by repeated sampling over several hours of a single day. Separate studies by B. Yoder and colleagues have demonstrated hydraulic limitation at the top of the old tree during conditions of midday summer drought, and these results suggest that the associated photosynthetic downregulation is detectable with spectral reflectance. These results suggest that different levels of physiological performance in complex landscapes can be characterized by remote narrow-band spectrometry. Data from Gamon and Yoder (in preparation).

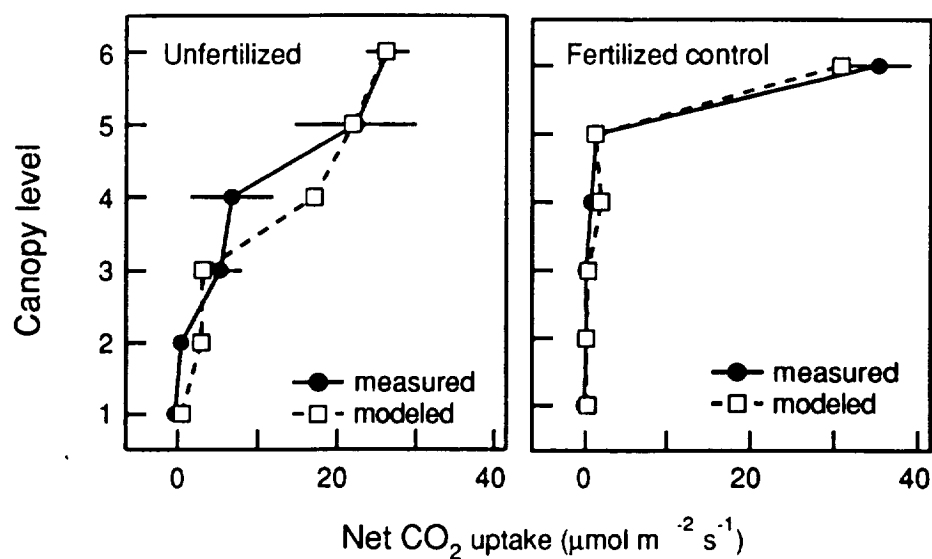


Figure 6. Measured and modeled photosynthetic rates for different layers of fertilized and unfertilized sunflower canopies. Measured rates were determined with a portable gas exchange system, and modeled rates were determined from reflectance and light measurements according to equation 1 (above). Efficiency was estimated from PRI using a relationship previously reported in Gamon et al. 1992. Data from Gamon, Field, Fredeen, Thayer (in preparation).